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The Anatomy of Cystodium

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Cystodium is a genus of little-known tree ferns containing a single species, *C. sorbifolium* (J. E. Smith) J. Smith, which is distributed in Malaysia. It grows only in lowland country and is adapted to a temperature of about 80°F all through the year, having continuous growth. The status of *Cystodium* as a genus distinct from *Dicksonia*, another genus of tree ferns, has often been questioned. Recent morphological and cytological studies by Holttum (1963) and Roy and Holttum (1965) indicate that the two genera are indeed distinct. Christensen (1938) and Copeland (1947) considered *Cystodium* to be probably derived from *Dicksonia*. The anatomy of *Dicksonia* is now well known (Holttum and Sen, 1961, and Sen, 1965), but this is the first detailed account of the anatomy of *Cystodium* yet published.

Material was collected by Prof. R. E. Holttum during his visit to New Guinea in 1963, and was sent to us by Mr. J. S. Womersley of the Department of Forests at Lae. Specimens were fixed in FAA, and the usual method of paraffin sectioning was followed. Sections were stained with Orange G and Safranin.

The stem of *Cystodium* is usually creeping, rarely erect, and is unbranched and cylindrical with an obconical base. The lower part of the stem is covered with the remains of petioles of old leaves and with numerous roots. At the distal end of the stem there is a crown of several bipinnate leaves.

Both the stem and the leaves in the young condition are protected by multicellular, uniseriate hairs in various stages of development. These hairs are the only epidermal appendages.

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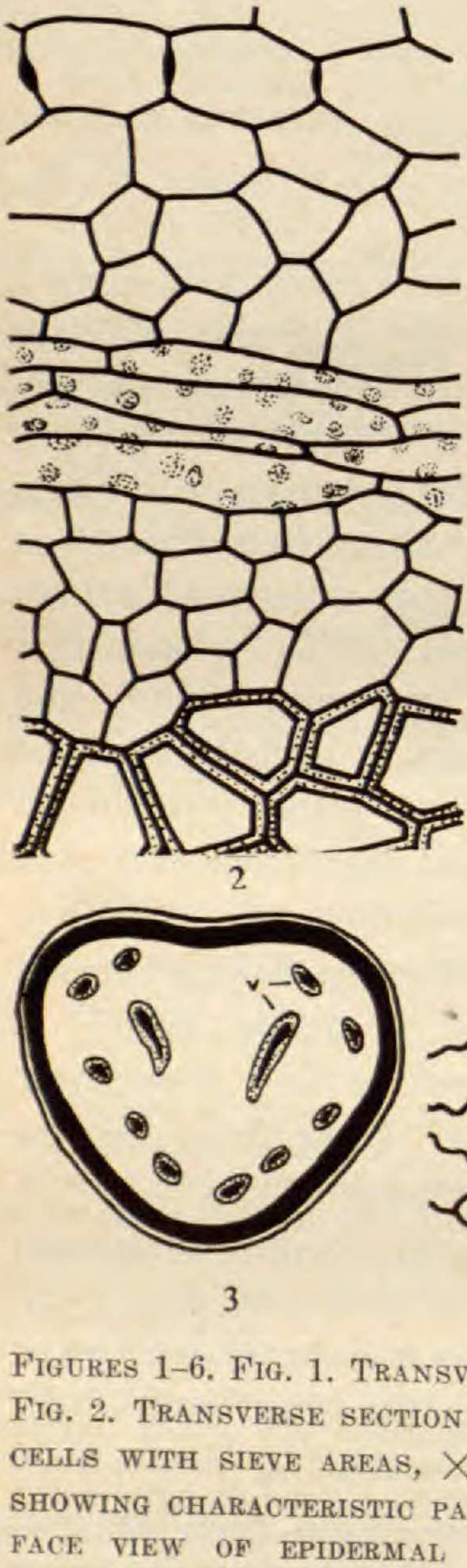

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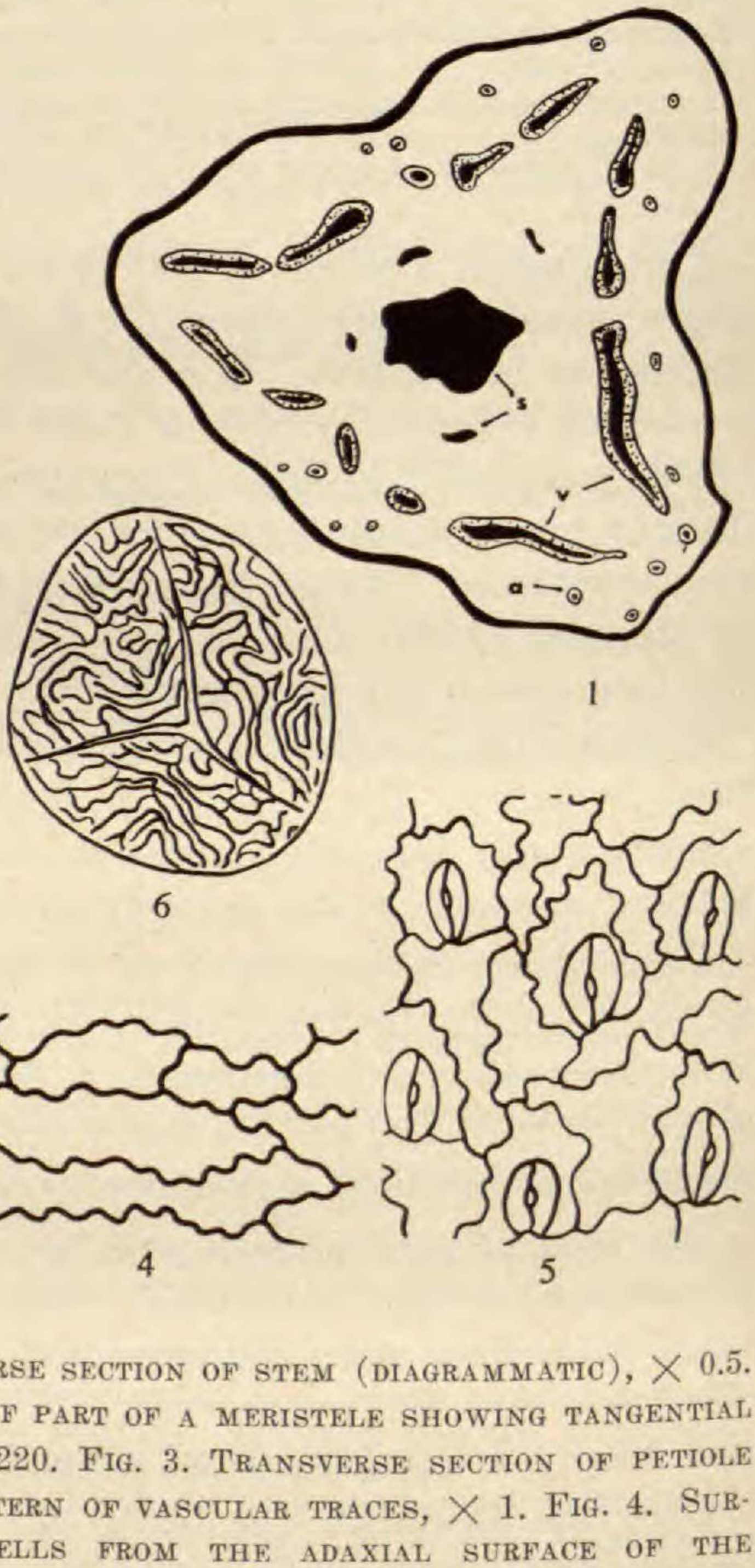

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Figures 1–6. Fig. 1. Transverse section of stem (diagrammatic), × 0.5. Fig. 2. Transverse section of part of a meristele showing tangential cells with sieve areas, × 220. Fig. 3. Transverse section of petiole showing characteristic pattern of vascular traces, × 1. Fig. 4. Surface view of epidermal cells from the adaxial surface of the lamina, × 80. Fig. 5. Surface view of epidermal cells from the abaxial surface of the lamina, × 80. Fig. 6. Proximal face of a spore, × 460. The abbreviations are: a = adventitious roots passing through the cortex, s = sclerenchymatous tissue, v = vascular tissue.

They are thin-walled and brown.

The internal structure of the stem is relatively simple. The epidermis is composed of elongated cells with slightly thickened external walls.

The cortex is differentiated into three zones: 1) the outer zone consists of vertically elongated parenchyma, the cells of which in the older stems are heavily lignified, and are then barely distinguishable, when viewed in cross section, from 2) the middle sclerenchymatous fibrous layer; towards the center this zone gradually merges into 3) an inner parenchymatous zone composed of thin-walled cells with intercellular spaces. This inner zone contains many irregularly distributed patches of sclerenchyma.

The vascular cylinder in an adult stem is dictyostelic (*Fig. 1*). The meristeles are surrounded by an endodermis, which is of a secondary type. The parenchymatous pericycle is about three cells thick. The phloem cannot be differentiated into proto- and metaphloem, but the sieve cells adjoining the pericycle are elongated tangentially as seen in a transverse section (*Fig. 2*). Hence they are cut transversely in a radial longitudinal section. These tangential cells often form a layer three or more cells deep. The xylem consists of scalariform tracheids and parenchyma, vessels being absent. The tracheids often show elongated to almost circular pits. The parenchymatous pith contains several irregularly distributed patches of sclerenchyma.

The petiole is slightly grooved on its adaxial surface. A dozen or more leaf traces enter the petiole. *Figure 3* is a transverse section showing the typical pattern of these bundles. Pneumathodes form an irregular line on either side of the petiole along the shoulders of the adaxial surface.

The epidermal cells on the adaxial surface of the lamina (*Fig. 4*) are sinuous and are more elongated than those of the abaxial surface. Stomata, which are confined to the abaxial surface, are of the syndetocheilic type, having one or two subsidiary cells associated with a pair of guard cells (*Fig. 5*).

The pinnules are slightly dimorphous. The sterile ones are serrate, while the fertile ones have a slightly narrower lamina and have enlarged teeth that form the adaxial lips of the indusia. The adaxial lip of the indusium is not very different from the lamina proper in having stomata and intercellular spaces, but the abaxial one is very delicate, and is without such structures. The receptacles are slightly raised and are circular in transverse section. The spores are tetrahedral and are ornamented with a delicate network of irregular ridges (*Fig. 6*).

Anatomical characteristics suggest that *Cystodium* and *Dicksonia* are sharply distinct. The cortex of the stem of *Dicksonia* is composed of five distinct layers, while in *Cystodium* it is of three layers. Several islets of parenchyma are found within the second layer of the cortex of *Dicksonia*, but these are absent from *Cystodium*. Cubical cells and mucilage cells are found in *Dicksonia*, but not in *Cystodium*. The receptacle is flattened or slightly raised and distinctly elongate in *Dicksonia*, whereas it is slightly raised and circular in *Cystodium*. The orientation of the subsidiary cells and guard cell mother cells is different in the two genera. The spore walls in *Dicksonia* are thick, especially at the angles, which are truncate, and the exine may be smooth, faintly granulate, or verrucate. In *Cystodium* the spores are ornamented with a delicate network of irregular ridges.

In view of these differences it seems unlikely that *Cystodium* is a direct descendant of *Dicksonia*. In spite of these differences, however, these two genera share many fundamental and peculiar characters: the sieve cells adjoining the pericycle are tangentially elongated, hairs are the only epidermal appendages, the leaves are dimorphous, leaf traces form a characteristic pattern common to both genera, the sori are marginal, and the indusia are two-lipped. Morphological characteristics of the gametophyte (Atkinson, 1965) are also significant. These and other characteristics justify keeping these two genera as members of the Cyatheaceae (*sensu* Holttum & Sen, 1961) and do not contradict the possibility of their origin from a common ancestor.

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Illustrations of Transient Fern Forms

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In the winter of 1964, Professor R. B. Channell of Vanderbilt University sent me an extraordinary plant of the walking-fern (*Camptosorus rhizophyllus*) which had been discovered by one of his students. The specimen appeared to have a dozen leaves altogether, but in fact it had only two. The pair of leaves were each repeatedly forked close to their blade bases so as to produce an apparent "spray" of many leaves, each of them with the typical long-attenuate tip. In classical taxonomy such a specimen as this might well have been described and given a latin name as a new form. Fortunately, Dr. Channell had the foresight to send the plant in question alive, so that we could carry out the experiment to be described below.

The specimen was originally discovered by Mr. Paul Weatherby on 27 November 1964, growing on a bluff about two miles south of Ashland City on River Road, across the Cumberland River from Marrowbone Creek, Cheatham County, Tennessee. Examples of the original leaves and those which resulted from the procedures of growing the plant will be deposited in the